

OBSERVATIONS ON AN ISOLATED POPULATION OF *SAGITTA HISPIDA* CONANT (CHAETOGNATHA) IN A TROPICAL LAGOON SYSTEM OF NORTHEAST YUCATAN (MEXICO)

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ABSTRACT Monthly zooplankton collections were carried out from January to December 1991 at two sampling sites, Cuenca Norte and Bojórquez lagoon, in the Nichupté lagoon system, a partially enclosed network of interconnected waterways located in the northeastern region of the Yucatan Peninsula (Mexico) adjacent to the Caribbean Sea. Only one species of Chaetognatha, *Sagitta hispida* Conant, was present and was more abundant at Cuenca Norte (total density 450.6 organisms/m³) than at Bojórquez (138.6 organisms/m³). The latter site is smaller, more physically isolated, and more environmentally stressed than the former. From monthly gonadal and length-frequency analyses of 1390 specimens, it was found that (1) total length significantly differed among four successive maturity stages, (2) juvenile and immature specimens occurred in greater numbers at Bojórquez, while more mature specimens comprised a greater percentage of individuals found at Cuenca Norte, and (3) individuals collected at Bojórquez, where slightly higher temperatures were recorded, were significantly smaller than those from Cuenca Norte. The latter two findings indicate that *Sagitta hispida* spawns at a higher frequency at Bojórquez, possibly due to the cumulative effect of higher temperature.

INTRODUCTION

Chaetognaths are among the most abundant holoplanktonic animals in oceanic, neritic and coastal environments (King 1979; Øresland 1990). Like most other zooplankters, chaetognaths produce more generations at lower latitudes where temperatures are higher (Dunbar 1941, 1952, 1962; McLaren 1963; Alvarifio 1965; Sameoto 1971). This higher breeding frequency has an impact on the composition of other zooplankters such as copepods which are reported to be their main prey item (Reeve 1970; Szyper 1978; Pearre 1980; Canino and Grant 1985; Alvarez-Cadena 1993).

Sagitta hispida Conant, 1895, is a conspicuous chaetognath commonly occurring in neritic waters on both sides of the tropical-equatorial Atlantic Ocean (Alvarifio 1965). It has often been reported as abundant in coastal waters of the Gulf of Mexico (Pierce 1951; McLelland 1989), along the east coast of the United States (Pierce 1953; Pierce and Wass 1962; Owre 1960; Grant 1962, 1963) and from some areas of the Caribbean Sea (Suárez-Caabro 1955; Michel 1984; Suárez-Morales et al. 1990; McLelland and Heard 1991; McLelland et al. 1992). In tropical regions, especially in areas with dense submerged vegetation, *Sagitta hispida* has been observed with a near bottom distribution (Owre 1972; McLelland and Heard 1991) leading Bieri (1991) to consider the species as

"quasi-planktonic". Other field studies demonstrate a marked diel migration for the species; mature specimens are rarely collected in surface waters during the day (McLelland and Heard 1991). Sweatt and Forward (1985) determined in laboratory studies that *S. hispida* demonstrates all-or-none upward vertical movement when ambient light intensity is below approximately $10^{16.7}$ photons m⁻² s⁻¹.

There are no previous reports on the chaetognath fauna in the Nichupté lagoon system (NLS), located on the Mexican coast of the Caribbean Sea. In this paper, we document the unique occurrence of *Sagitta hispida* in this lagoon system and compare the populations of the species at two sites with differing hydrological conditions, while considering data on body length and four preadult maturity stages.

STUDY AREA

The NLS is located adjacent to the Caribbean Sea (21° 07'N, 86° 46'W) in the northeastern region of the Yucatan Peninsula (Figure 1). The climate in the region is subhumid and warm (lowest temperatures are higher than 18°C) with the main rainy season in summer and moderate rainfall in winter (type AW1 (X')(i') g of García 1964). Although the NLS (type IV-B of Lankford 1976) at present is largely surrounded by tourist facilities, it was originally bordered by mangrove vegetation. In tropical oligotrophic

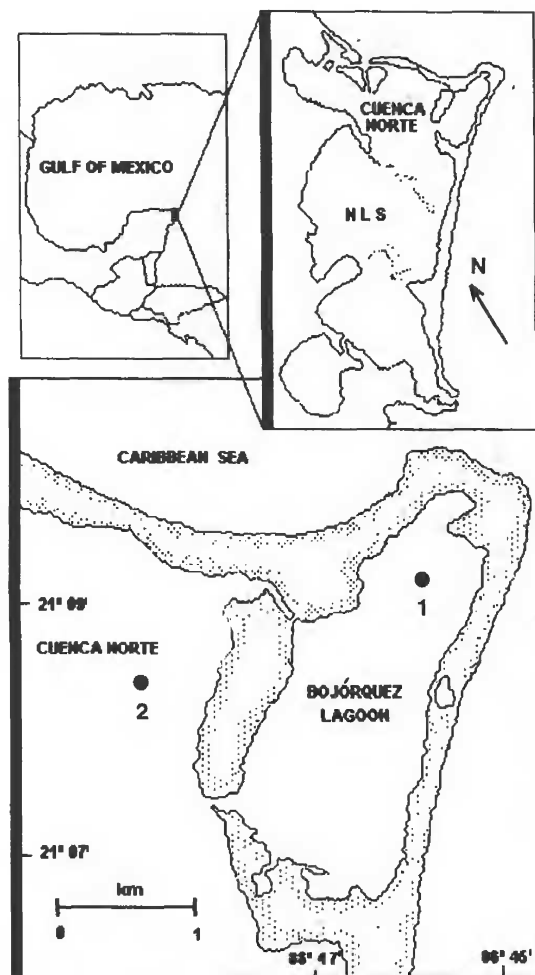


Figure 1. Study area and sampling sites in the Mexican Caribbean.

systems such as NLS, the typical submerged vegetation is characterized by *Thalassia testudinum*, *Halodule* sp. and rhizophytic or calcareous algae. The soil in the area is highly porous and permeable (Butterlin 1958; López-Ramos 1974). Freshwater runoff from rivers that typify other lagoon systems is lacking. Subterranean springs and "cenotes" (karstic water deposits) provide variable amounts of freshwater input into the system.

Three climatic regimes are reported annually in this area: "nortes", dry, and rainy seasons (Merino and Otero 1991). During the present study period (1991), "nortes", identified by the strong northern winds which blow in the area, extended from December to March. The dry season, with dominant southeastern winds and low precipitation,

extended from April to July. The rainy season, with the same wind pattern but higher precipitation, extended from August to November.

For this study, two intrinsically different sampling areas at adjacent locations within the NLS (Figure 1) were compared. Station 1 consisted of two sites in Bojórquez lagoon, a nearly enclosed, shallow (1.5 m average depth) lagoon with two narrow openings to other parts of the NLS. Bojórquez lagoon is further characterized by high salinity, nutrient enriched water from organic pollution, and patches of *Thalassia testudinum* and *Halodule*. Anthropogenic stress at this site is considerable and was detailed by Alvarez-Cadena and Segura-Puertas (in preparation). Station 2 was located in Cuenca Norte, a larger, less stressed body of water averaging 2.5 m in depth and with a small, but distant opening to the Caribbean Sea to the north. Of the two, station 2 is, on the whole, more representative of the NLS.

MATERIALS AND METHODS

Zooplankton samples and surface hydrographic data (salinity and temperature) were collected at the two stations monthly from January to December 1991. All collecting was performed between 0900 and 1100 hrs. A conical plankton net (0.42 m diameter, 330 μ m mesh) was equipped with a General Oceanics flowmeter and towed in a circular path near the surface for 5 minutes at 1.5 knots. Samples were preserved in the field with buffered (lithium carbonate) formalin at a concentration of 5% formalin-seawater. In the laboratory, all chaetognaths collected were counted and examined for species identification, whereupon at least 50 animals were randomly removed from each sample, measured to the nearest 0.1 mm, and examined for gonadal condition. Measurements were made from the tip of the head to the tail excluding the tail fin. Maturation stages were assigned as follows and were based on various classifications reviewed by Alvariffo (1965):

Stage I. Ovaries not visible, or if present are very small, not reaching anterior part of posterior fin; few small oocytes present. Seminal vesicles not present and no sperm visible in tail segment.

Stage II. Ovaries visible, usually reaching mid space between lateral fins or posterior part of anterior fin; small oocytes present. Some thickening occurring near end of posterior fin indicating primordium of seminal vesicles; sperm present but not occupying entire tail segment.

Stage III. Ovaries reaching midpoint of anterior fin; oocytes rounded. Seminal vesicles visible but somewhat flattened; sperm present throughout tail segment.

Stage IV. Ovaries reaching anterior part of anterior fin; oocytes rounded, arranged usually in two rows. Seminal vesicles oval to rectangular, testes full of sperm.

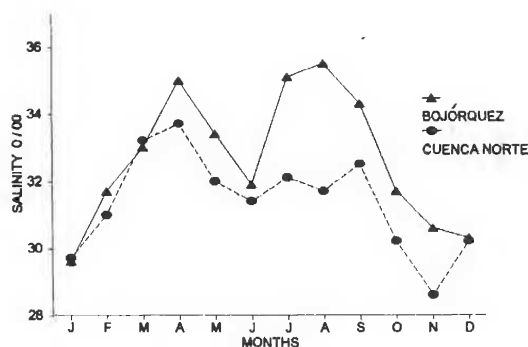


Figure 2. Annual variation of salinity at Bojórquez and Cuenca Norte. Bojórquez data are mean values recorded from two sampling sites.

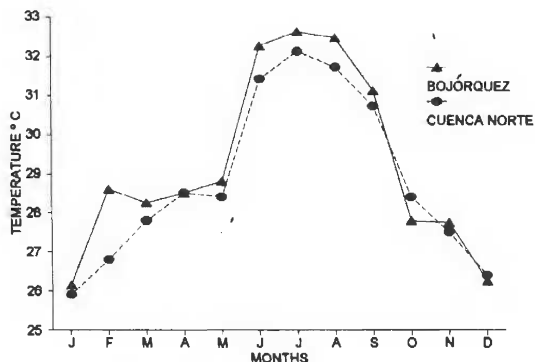


Figure 3. Annual variation of temperature at Bojórquez and Cuenca Norte. Bojórquez data are mean values recorded from two sampling sites.

Stage V. Ovaries reaching posterior part of ventral ganglion, oocytes fully matured. Seminal vesicles completely full or sometimes "spent" (empty).

Chaetognath data from the two sites in Bojórquez were pooled as the mean lengths of the animals did not show any significant differences. Likewise, pooled values are given for salinity and temperature recorded from Bojórquez (Figures 2,3).

Data from the two stations were compared statistically using mean length measurements (total N=1390) for maturity stages I-IV. A two-way analysis of variance (ANOVA) was used to test for variation among stages at each station and for differences between stations. A t-test was employed to further compare the differences among the mean lengths of each maturity stage between the two stations. Testing was performed at $\alpha=0.05$ with confidence intervals of 99%.

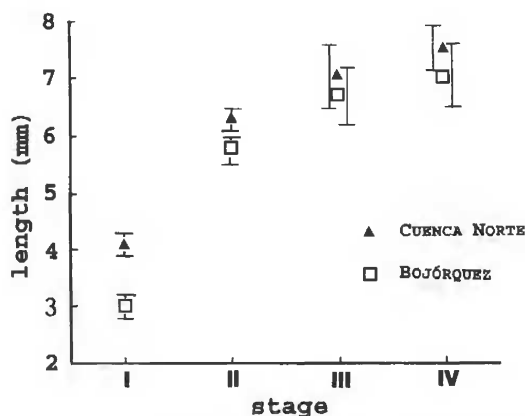


Figure 4. Annual mean length variations of *Sagitta hispida* maturity stages I-IV at Cuenca Norte and Bojórquez.

RESULTS

Salinity at Bojórquez was usually higher than at Cuenca Norte (Figure 2). Lower salinity was observed at both stations during January ("nortes") with 29.63 and 19.72‰ respectively. Highest values were recorded in August for Bojórquez (35.44‰) and in July for Cuenca Norte (34.68‰). Temperature was usually slightly higher at Bojórquez than at Cuenca Norte (Figure 3). At both stations, the lowest temperature was recorded in January and the highest in July-August.

The taxonomic analysis of chaetognaths collected at both sites during the survey revealed the presence of only one species, *Sagitta hispida*. It was about three times as abundant at Cuenca Norte (450.6 organisms/m³) than at Bojórquez with a total density of 138.6 organisms/m³ (Table 1). Proportionally, stage I was the most common of all maturity stages, and comprised a higher percentage of the population at Bojórquez (89.2%) than at Cuenca Norte (71.2%). Stages II to IV were consistently higher in percentage at Cuenca Norte than at Bojórquez (14.1% stage II, 6.4% stage III, and 8.3% stage IV from Cuenca Norte and 7.6% stage II, 1.8% stage III, and 1.4% stage IV for Bojórquez). Only seven adult specimens of stage V (8.5-9.0 mm total length) were collected during the survey, six at Cuenca Norte and one at Bojórquez. Because of this extreme scarcity, comparative analyses were omitted for this stage.

Mean lengths were variable during the annual cycle (Table 2, Figures 4, 5a and 5b), especially those of stage I at Bojórquez which ranged from 1.59 mm in August to > 4 mm in March, April and November (variation range = 64%). Stage I animals at Cuenca Norte did not show this range of size variability (3.18 mm in May to 4.8 mm in August; variation range 33%). The mean lengths of the remaining stages showed less variability at both sampling areas.

TABLE 1

Numbers analyzed monthly for maturity stages I-IV and total density (organisms/m³) of *Sagitta hispida* at Bojórquez and Cuenca Norte. Data for Bojórquez represent pooled values from two sites.

Bojórquez

Stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total (org./m ³)	%
I	49	82	41	16	70	80	82	78	98	72	40	18	726	89.2
II	0	8	8	9	1	2	1	13	2	13	5	0	62	7.6
III	0	0	0	2	1	0	1	5	0	3	3	0	15	1.8
IV	1	0	1	1	0	0	0	4	0	2	2	0	11	1.4
Org./m ³	11	5.9	3.1	2.1	4.1	15.3	5.1	39.5	19	13.5	13	6.3	138.6	-

Cuenca Norte

Stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total (org./m ³)	%
I	29	30	38	39	21	37	42	18	35	44	35	42	410	71.2
II	11	12	8	8	0	7	1	9	7	3	7	8	81	14.1
III	5	6	2	2	0	2	4	6	4	1	5	0	37	6.4
IV	5	2	2	1	0	4	3	17	9	2	3	0	48	8.3
Org./m ³	5	9.6	12.5	15.8	44.3	82.5	49.4	133.3	17.9	0.3	31	49	450.6	-

Length data for each stage at the two sites (1390 measurements) were tested using a two-way analysis of variance (ANOVA) for variation in mean length in sampling sites vs. the four maturity stages. Residual data showed a normal distribution with the Kolmogorov-Smirnov test. It was found that significant differences ($\alpha=0.05$) existed in length vs. sampling site ($F_s=9.55$, $p=0.002$), maturity stage ($F_s=227.97$, $p<0.001$), and interaction between the two factors ($F_s=13.12$, $p<0.001$). It was further found that total length significantly differed among successive maturity stages and that individuals collected at Cuenca Norte were significantly larger than those caught at Bojórquez for each of the four maturity stages (Figure 4). Both parameters were constant at all levels and the terms of significant interaction were not evident, but could be explained by the larger difference between stage I lengths at both sampling sites (Figure 5a,b).

In order to compare mean length differences of each maturity stage between the two sampling sites, t-tests were used with confidence intervals of 99% and testing H_0 at $\alpha=0.05$. For stage I, with 1136 individual length measurements (410 from Cuenca Norte and 726 from Bojórquez), differences were highly significant ($t=-17.58$), exhibiting the widest range of difference between the two sampling areas. For stage II, with less available data ($N=143$), differences were also significant ($t=-3.46$). However, the same analyses with stage III and IV data revealed no differences at 99% C.I. between the lengths of Cuenca Norte and Bojórquez specimens. Finally, when this analysis was performed pooling the total number of observations (1390) from all stages at each station group, the differences were found to be significant ($t=18.58$) between the two sampling areas.

TABLE 2

Monthly mean length (mm) of *Sagitta hispida* for maturity stages I-IV at Bojórquez and Cuenca Norte. Data for Bojórquez represent pooled values from two sites.

Bojórquez

Stage	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Grand Mean
I	2.61	2.77	4.17	4.72	3.32	2.62	2.17	1.59	2.98	2.53	4.36	3.34	2.956
II	---	5.66	5.87	6.44	5.70	---	---	---	---	---	5.56	---	5.761
III	---	---	---	7.00	5.50	---	---	---	---	---	6.76	---	6.660
IV	7.45	---	6.90	---	---	---	---	---	---	---	8.00	---	7.070

Cuenca Norte

Stage	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Grand Mean
I	4.27	4.72	4.28	4.14	3.18	3.21	3.68	4.77	4.46	4.23	4.46	3.34	4.181
II	6.10	6.84	6.21	6.01	---	5.13	6.00	6.61	6.02	6.40	6.01	---	6.251
III	7.48	7.80	6.70	6.90	---	6.00	6.65	6.98	7.02	6.70	6.40	---	6.985
IV	8.10	7.25	7.76	7.70	---	6.54	7.13	7.34	7.57	7.70	7.76	---	7.481

DISCUSSION

Identification of immature chaetognaths is often difficult and confusing because of their small size and undeveloped, taxonomically important sexual features. This is particularly complicated in localities where several species co-occur. *Sagitta hispida*, however, can be readily identified by its conspicuously large, wide head, square to bean-shaped eye pigment and the presence of gut diverticulae in larger specimens (McLelland 1989). Immature specimens can be distinguished from similar species by examining the anterior teeth which, under high magnification, appear to lie flat against the head, their tips forming a line nearly perpendicular to the body axis; furthermore, the teeth have longitudinal ridges which give them a quadrangular cross-sectional appearance. These ridges can be seen in SEM photographs by Cospér and Reeve (1970). In mature specimens, the ovaries often extend past the midpoint of the anterior fins and contain round ova arranged in two rows. The lateral fins are completely rayed, with the posterior fins reaching the seminal vesicles. The latter are oval to rectangular when ripe, and separated from the caudal fin by half their length.

Sagitta hispida has been reported to tolerate wide ranges of salinity and temperature. Experiments by Reeve

and Walter (1972) on growth rates in laboratory populations found that the species will not survive more than 15 days at temperatures above 33.5°C. They also found that the species can grow to maturity in salinity ranges from 25-40‰, but failed to mature at 20‰ and below. At both stations in the NLS, temperatures were never below 25°C or above 33°C. On the other hand, salinities were not below 28‰ or above 36‰. Thus, the ranges were well within the known ranges of growth and maturation and may explain the local success of *S. hispida*. The fact that the species was represented in our samples mainly by immature specimens likely indicates a combination of continuous spawning of the population, a greater mortality of older individuals, and the known differential vertical distribution of juvenile and adult chaetognaths. *Sagitta hispida* is known to breed more or less continuously throughout the year in tropical and subtropical waters (Pierce 1951; Owre 1960), resulting in a large proportion of immature specimens representing multiple generations coexisting at different stages of development (Pearre 1991). A concentration of immature chaetognaths in the upper water column is thought to be an indication of shallow-water spawning (Stone 1969) or better survival conditions for younger individuals (Raymont

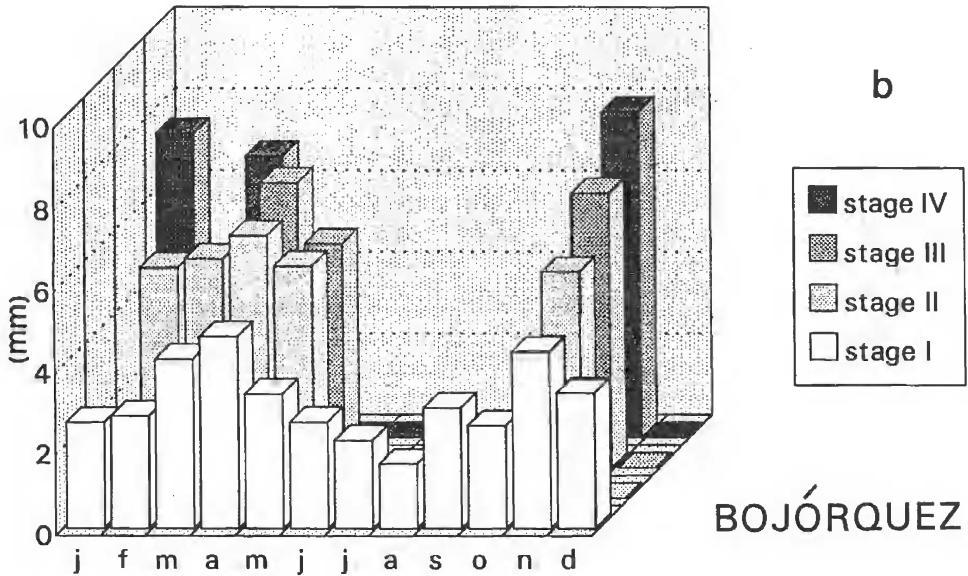
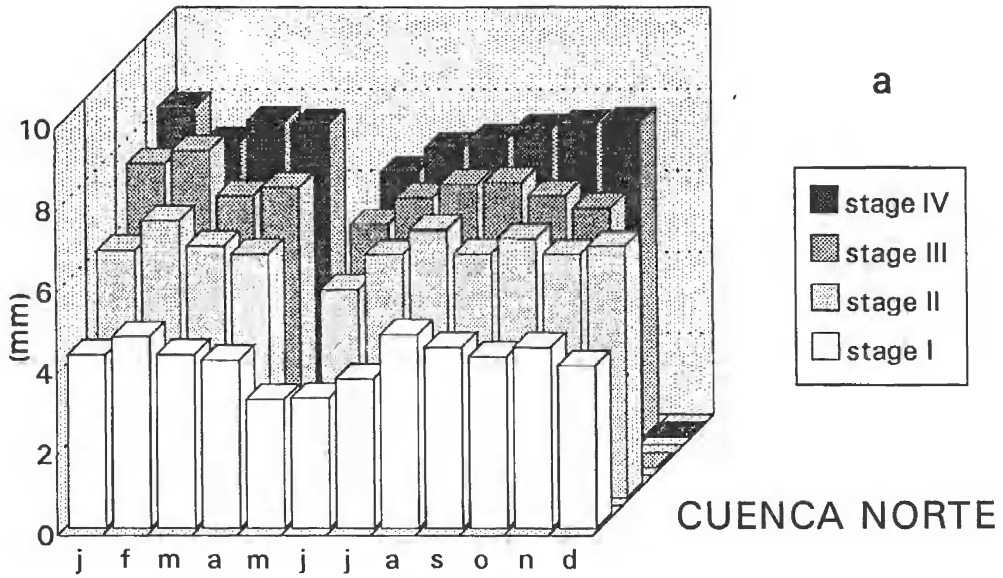


Figure 5. Monthly mean length of *Sagitta hispida* maturity stages I-IV at Cuenca Norte and Bojórquez.

1963; McLelland 1984). Adults of *S. hispida* have been reported to dwell near the bottom or associate with submerged seagrass beds during the day (Owre 1972; Sweatt and Forward 1985; McLelland and Heard 1991) and migrate upward at night. Although our sampling efforts were near the surface, our data confirms that young individuals can be found abundantly in the water column even during the day. In additional samples (not reported here) collected over a 24-hour period in April and October in Bojórquez lagoon, larger numbers of adult animals were collected at night, further supporting the assumption of diel migration for this species.

The statistical analyses of length variations in the surveyed populations of *Sagitta hispida* clearly showed that (1) successive maturity stages are well defined in regards to corresponding body length, (2) differences between sampling stations were more apparent in stages I and II, and (3) Cuenca Norte individuals were consistently larger at all stages as compared to those from Bojórquez. Food availability did not seem to be the reason for differences in size between the two stations. In a concurrent study, Alvarez-Cadena and Segura-Puertas (in preparation) found that copepods in Bojórquez, where chaetognaths were smaller, were nearly three times as abundant as those of Cuenca Norte (6177.6 and 2236/m³ respectively, annual abundance). On the other hand, it is possible that when food is overly abundant, the metabolic energy of the chaetognath is shifted to reproductive output instead of growth, accounting for a smaller size at maturity (faster rate of maturation) at Bojórquez. The two dominant genera of the NLS copepod population, *Acartia* and *Paracalanus*, were reported by Reeve (1966) to be the main food items for *S. hispida* in Biscayne Bay, Florida.

Temperature differences between the two stations might account for the observed dissimilarities in body sizes and relative proportions of maturity stages. For some zooplanktonic organisms, temperature seems to be related not only to the attainment of larger size at maturity, but also with the number of generations produced by the species. Dunbar (1941) mentioned that "it is generally true that zooplankters of high latitudes (colder waters) develop more slowly, reach larger size and live longer than related forms in warmer areas." McLaren (1963, 1966) reported that *Sagitta elegans*, a circumboreal species, required more time to reach maturity at lower temperatures. It may be argued that temperature differences between Bojórquez and Cuenca Norte are very small (on the order of 1°C or less) and not significant enough for these differences. However, the cumulative effect of temperature, rather than just the slightly higher values, may be responsible for the smaller mean size yet apparently higher spawning frequency of *S. hispida* at Bojórquez. Sameoto (1971) reported

that once *S. elegans* had accumulated 738°C degree-days, the species would reach maturity. Jakobsen (1971) remarked that small differences in temperature could promote distinct gonadal development due to the extent of the period they exerted their influence. Dunbar (1962) also found that although hydrographic differences (e.g., temperature) were not large, they also had a cumulative effect on the biology of *S. elegans*.

Reeve and Walter (1972) reported that *Sagitta hispida* completes its entire life cycle in 18 to 50 days. Although the number of generations for *S. hispida* cannot be accurately determined in this work because samples were collected at monthly intervals, apparently a higher number of generations is produced at Bojórquez than at Cuenca Norte as evidenced by the higher frequency of juveniles (stage I) recorded throughout the year. A more frequent sampling effort might clarify this.

The population of *Sagitta hispida* in the NLS, especially Bojórquez, is largely isolated from continual genetic input from coastal populations by the combined effects of low-energy tidal flow and poor circulation which hinder exchange with the adjacent marine environment. Residence of water in the NLS, as a whole, has been estimated at about two years (Merino et al. 1990), except for occasional catastrophic events such as Hurricane Gilbert in 1988 which overwashed the narrow land barrier separating the lagoon system from the Caribbean Sea. In Bojórquez, wind-aided circulation has been further diminished by the dense line of hotels and other tourist facilities along the Caribbean seacoast which obstruct the dominant southeast trade winds from reaching the lagoon. In a personal communication to the second author, S. Van der Spoel suggested that tangible variations begin to appear in a typical planktonic species population that has been isolated for 200 generations. Given a more or less continual rate of growth and a generation turnover of 20-30 days for *Sagitta hispida*, such population divergences should occur within 10-15 year intervals. Thus, it is possible that because of its isolation, a population of *Sagitta hispida* characterized by smaller adults is evolving in Bojórquez lagoon.

ACKNOWLEDGMENTS

We wish to thank F. Escobar de la Llata for helping with the map and some of the figures. F. Ruiz-Rentería and Ma. E. Islas-Landeros collaborated during the field sampling and salinity determinations. This paper was substantially improved by the comments of anonymous reviewers.

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